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Relationships between root density of the African grass *Hyparrhenia diplandra* and nitrification at the decimetric scale: an inhibition–stimulation balance hypothesis

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Previous studies have shown that Lamto savannah exhibits two different types of nitrogen cycle with high and low nitrification sites and suggested that the perennial grass *Hyparrhenia diplandra* is responsible for this duality at a subpopulation level, with one ecotype being thought to be able to inhibit nitrification. The present work aimed to investigate the relationships between nitrification and the roots of *H. diplandra* at two scales. (i) Site-scale experiments gave new insight into the hypothesized control of nitrification by *H. diplandra* tussocks: the two ecotypes exhibited opposite influences, inhibition in a low nitrification site (A) and stimulation in a high nitrification site (B). (ii) Decimetric-scale experiments demonstrated close negative or positive relationships (in sites A or B, respectively) between the roots and nitrification (in the 0–10 cm soil layer), showing an unexpectedly high sensitivity of the nitrification process to root density. In both soils, the correlation between the roots and nitrification decreased with depth and practically disappeared in the 20–30 cm soil layer (where the nitrification potential was found to be very low). Therefore, the impact of *H. diplandra* on nitrification may be viewed as an inhibition–stimulation balance.

Keywords: *Hyparrhenia diplandra*; Lamto; roots; nitrification potential; savannah

1. INTRODUCTION

The process of nitrification, which is responsible for the transformation of ammonium into nitrate, plays an important role in ecosystem functioning and particularly in nutrient-limited ones such as the wet savannah of Lamto (Côte d'Ivoire, West Africa). Indeed, it is involved in the control of (i) nitrogen plant nutrition and (ii) nitrogen losses from the ecosystem (Vitousek *et al*. 1979; Keeney 1986; Robertson 1989). In Lamto savannah, nitrification is known to be highly heterogeneous in space and strongly patchy, with high and low nitrification sites within the same ecosystem (Le Roux *et al*. 1995; Lata *et al*. 1999). The perennial Graminaceae (Poaceae) *Hyparrhenia diplandra* is the dominant grass of Lamto savannah. This plant is structured in tussocks separated by bare soil (with *ca*. 0.5 m between individuals). *Hyparrhenia diplandra* has been suspected of being responsible for the dual functioning (low and high nitrification) of the system at a subpopulation level: it was hypothesized that the *H. diplandra* subpopulation from low nitrification sites is able to suppress nitrification, while the subpopulation of high nitrification sites is unable to express this ability (Lata *et al*. 1999).

The production of allelopathic compound(s) by the roots of the *H. diplandra* subpopulation from the low nitrifying sites has been proposed as the more probable hypothesis for explaining the virtual lack of nitrification (Lata *et al*. 1999). The depressive effect of *H. diplandra* upon nitrification has already been reported by Meiklejohn (1962, 1968), Munro (1966) and Rice & Pancholy (1973). However, this hypothesis has remained controversial for a long time since no clear *in situ* evidence has been provided.

In the present paper, the influence of the roots of *H. diplandra* on nitrification was assessed at two scales. On the site scale, we compared the soil nitrification potential in low or high nitrifying sites (0–10 cm layer) and under or between randomly chosen tussocks. On the decimetric scale, the correlations between the location of the *H. diplandra* tussocks, root biomass and nitrification potential were studied. This was performed on 1-m transects designed on two sites. At this same decimetric scale, this study was completed by investigating the effect of soil depth on the root biomass–nitrification relationship by the use of a random sampling procedure.

2. MATERIAL AND METHODS

(a) *Site description*

Lamto is located in Côte d'Ivoire (West Africa) at latitude 6°13′ N and longitude 5°20′ W at the southward limit of the 'V Baoulé', a broad grass expanse of savannahs which spreads southwards far into the rainforest. The vegetation varies with the topography and five facies, from downslope to upslope, can be distinguished on the basis of tree density and main grass species (Devineau 1976; Menaut & César 1979); these are (i) a riparian forest along the Bandama river, (ii) gallery forests in the thalwegs, (iii) herbaceous savannah, without trees other than the palm *Borassus aethiopum*, dominated by the grasses *Loudetia simplex* and *Andropogon schirensis*, (iv) shrub savannah dominated by the grasses *H. diplandra* and *Hyparrhenia smithiana*, and (v) dry semi-deciduous forests on the plateaux.

Temperatures are constant throughout the year (average 27 °C). Rainfall is variable and four seasons can be

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Table 1. *Soil physicochemical characteristics of the low and high nitrifying sites at different soil depths (0–10, 10–20 and 20–30 cm)*

(The values are presented with standard errors in parentheses. There was no difference between sites A and B for all variables at the same depths at the $p = 0.05$ level.)

site	depth (cm)	total sands (%)	total silts (%)	total clays (%)	total nitrogen[a]	total carbon[a]	C:N
site A	0–10	78.23 (1.85)	13.18 (2.87)	8.59 (1.60)	0.55 (0.07)	9.2 (0.8)	16.7
	10–20	77.86 (1.68)	13.71 (1.05)	8.43 (1.19)	0.59 (0.04)	8.7 (0.5)	14.7
	20–30	76.49 (1.60)	15.22 (2.32)	8.28 (2.37)	0.54 (0.02)	7.5 (0.4)	13.9
site B	0–10	75.51 (2.49)	16.60 (1.40)	7.89 (1.39)	0.63 (0.08)	10.5 (0.6)	16.7
	10–20	76.98 (1.28)	14.50 (1.28)	8.52 (1.04)	0.60 (0.05)	8.6 (0.4)	14.3
	20–30	75.62 (1.79)	14.01 (1.27)	10.37 (0.97)	0.52 (0.04)	7.2 (0.3)	13.8

[a] Expressed in mg g^{-1} dry soil.

distinguished: (i) the long dry season from December to February, (ii) the long wet season from March to July, (iii) the short dry season in August, and (iv) the short wet season from September to November. Precipitation averages 1200 mm (statistics from Geophysical Station of Lamto). The soils are composed of granites and derived sands and are classified as tropical ferrugineous soils with a superficial gravely horizon.

We confined our study to the shrub savannah, which is the dominant biotope and which covers almost 55% of the surface of the Lamto reserve (Gautier 1990).

(b) *Soils studied and sampling procedures*

Soils were sampled during the long wet season (March–April 1997) in two savannah sites (5 km apart and more than 2.5 ha each), both strongly dominated by the perennial *H. diplandra*: reference site A, where the nitrification potential has been shown to be low in previous studies (Abbadie *et al*. 1992; Lensi *et al*. 1992; Le Roux *et al*. 1995; Lata *et al*. 1999) and reference site B, where a high nitrification potential has been found (Le Roux *et al*. 1995; Lata *et al*. 1999). No significant differences were observed between the two sites in both the 0–10-cm-layer soil characteristics and in plant species composition (Lata *et al*. 1999). The main physicochemical characteristics of the soils of both sites at depths of 0–10, 10–20 and 20–30 cm are given in table 1. The soils were expectedly sandy and slightly acidic with pH KCl values of around 6 (6.82 (0.26) and 6.74 (0.08) at 0–10 cm depth for sites A and B, respectively).

In the site-scale sampling, 25 soil samples (*ca*. 500 cm^3 each) were randomly collected from the 0–10 cm layer under and between the *H. diplandra* tussocks at each site (total number of samples, 100).

In the first decimetric-scale sampling, ten cubes of 10 cm × 10 cm × 10 cm of soil were sampled in the 0–10 cm layer along a 1-m transect at each site. The main criterion for choosing transect locations was to include adjacent areas covered by *H. diplandra* and uncovered areas along the transect.

In the second decimetric-scale sampling, 35 cubes (10 cm × 10 cm × 10 cm) of soil were randomly collected at three depths (0–10, 10–20 and 20–30 cm) at the two sites in an area of 1 m^2 including the previous transects. All samples were immediately air dried in the shade, homogenized, sieved (< 2 mm) and stored in sealed plastic bags for one month until the experiments. The roots were collected and weighed after sieving.

(c) *Enzymatic potential of nitrification assays*

The enzymatic nitrification potential was measured according to Lensi *et al*. (1986): the NO_3^- produced during an aerobic incubation was deduced from N_2O measurements after anaerobic incubation in the presence of C_2H_2.

Subsamples of 15 g ($n = 6$) from each soil sample were placed in 150 ml plasma flasks. Three subsamples were used to estimate the initial NO_3^- content: they were supplied with 6 ml of a suspension of a denitrifying organism (*Pseudomonas fluorescens*, $OD_{580} = 2$) in a solution containing glucose and glutamic acid (the final soil carbon content for each compound was 0.5 mg of carbon per gram of dry soil). This procedure ensures a high denitrifying potential and an excess of electron donors. The flasks were sealed with rubber stoppers and the atmosphere of each flask was replaced by a He:C_2H_2 mixture (90:10) to ensure anaerobic conditions and N_2O reductase inhibition. The N_2O accumulation was followed until a constant value (i.e. a total conversion of the soil NO_3^- content into N_2O) was reached.

The three other subsamples were used to determine the kinetics of NO_3^- accumulation: they were enriched with 2 ml of an $(NH_4)_2SO_4$ solution (final soil nitrogen content of 0.2 mg per gram of dry soil) in order to ensure a moisture content equivalent to 80% water holding capacity and no limitation by ammonium (the presence of NH_4^+ also limits NO_3^- assimilation by micro-organisms). Then, the flasks were sealed with parafilm® (which prevents soil from drying but allows gas exchange) and incubated at 27 °C for 48 h in a horizontal position to ensure optimal and homogeneous aeration of the soil. After this aerobic incubation, which allows nitrate to accumulate, the soil samples were enriched with 4 ml of a *P. fluorescens* suspension ($OD_{580} = 2$) in a solution containing glucose and glutamic acid (in concentrations adequate for achieving the same final soil carbon content as above). Then, anaerobiosis and N_2O inhibition were obtained in the flasks as described above and the N_2O accumulation was followed until a constant value was reached. We ascertained that neither nitrate nor nitrite remained in the *Pseudomonas* suspensions before they were added to the soil (i) by a colorimetry procedure using Morgan's and Griess Ilosway's reagents, and (ii) by anaerobic incubation of the suspension aliquots (with carbon and C_2H_2 supplies) in order to verify that no N_2O was produced.

N_2O was analysed on a gas chromatograph equipped with an electron capture detector. Previous studies (Abbadie & Lensi 1990; Lensi *et al*. 1992) have demonstrated that the nitrifying potential of different soils was not affected by drying and storage.

The enzymatic nitrification potential was computed by subtracting the nitrate initially present in the soil from the nitrate accumulated after aerobic incubation and expressed as nanograms of NO_3^--N produced per gram of dry soil per 48 h.

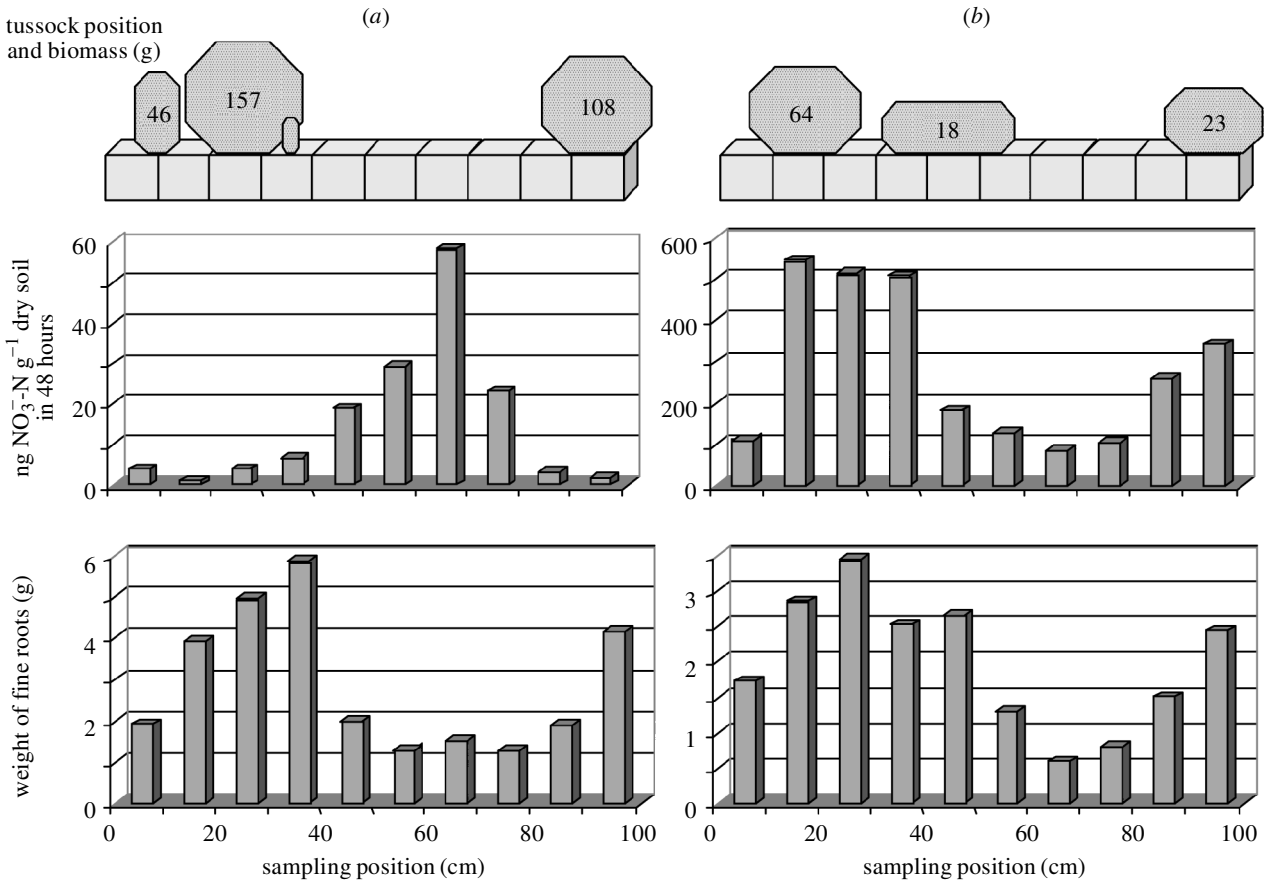

Figure 1. Transects in (*a*) the low nitrification site and (*b*) the high nitrification site, at the first depth (0–10 cm). From top to bottom. Tussock biomass in grams of dry material. Transect drawing with tussock location; each cube is 10 cm × 10 cm × 10 cm. Nitrification potential in nanograms of NO_3^--N produced per gram of dry soil per 48 h aerobic incubation. Total fine roots weight in grams.

(d) *Statistical analysis*

All statistical analyses were performed with SAS® software (SAS Institute, Inc. 1989). We used the PROC GLM procedure with the type III sum of squares for unbalanced analyses of variance and analyses of covariance. The LSMEANs procedure was used to compare the least-squares' means across levels of class variables. All tests were performed at the 0.05 significance level.

3. RESULTS

(a) *Comparison of the nitrification potential under and between* H. diplandra *tussocks*

The nitrification potential was significantly (d.f. = 99, $r^2 = 0.6728$, $F = 13.61$ and $p = 0.0001$) lower in site A than in site B. In the low nitrifying site, the nitrification potential was significantly ($p = 0.0001$) lower under than between the tussocks: the means ± s.e.m.s are 8 ± 2 and 75 ± 15 ng NO_3^--N produced per gram of dry soil per 48 h, respectively. In the high nitrifying site, the nitrification potential was significantly ($p = 0.0001$) higher under than between the tussocks: 430 ± 110 and 190 ± 70 ng g^{-1} 48 h^{-1}, respectively.

(b) *Relationships between root densities and nitrification potential along the 1-m transects*

Figure 1 shows that the fine root weight strictly matches the individual tussock position in the 0–10 cm layer of the two sites. The highest root densities were measured under the biggest tussocks and the lowest in the soil between the tussocks (d.f. = 59, $r^2 = 0.9304$, $F = 58.32$ and $p = 0.0001$). In the low nitrification site, the soil samples exhibited the lowest nitrification potential where the root weight was at its maximum ($p = 0.0001$). On the contrary, in the high nitrification site, the soil samples exhibited the highest nitrification potential where the root weight was at its maximum ($p = 0.0001$).

(c) *Correlations between the root densities and nitrification potential at three depths*

Figure 2 shows that the mean nitrification potential was significantly higher in site B than in site A at all depths (d.f. = 11, $r^2 = 0.9607$, $F = 439.88$ and $p = 0.0001$), and that the nitrification significantly decreased with depth within each site ($p = 0.0001$). The means (± s.e.m.s) of the nitrification potentials at depths of 0–10, 10–20 and 20–30 cm were, respectively, 13.39 ± 12.80, 1.09 ± 0.68 and 0.17 ± 0.09 ng NO_3^--N produced per gram of dry soil per 48 h for site A and 212.98 ± 144.49, 18.91 ± 10.21 and 11.08 ± 3.08 ng g^{-1} 48 h^{-1} for site B. The root density in the low nitrification site was significantly higher than in the high nitrification site at all depths ($p = 0.0001$) and the mean root density significantly decreased with depth within each site ($p = 0.0001$). The means (± s.e.m.s) of the root densities at depths of 0–10, 10–20 and 20–30 cm were, respectively, 4.04 ± 2.33, 0.97 ± 0.36 and 0.37 ± 0.12 g of grass root dm^{-3} for site A and 1.32 ± 0.91, 0.36 ± 0.17 and 0.21 ± 0.13 g dm^{-3} for site B. A significant correlation was observed in the two sites between the root

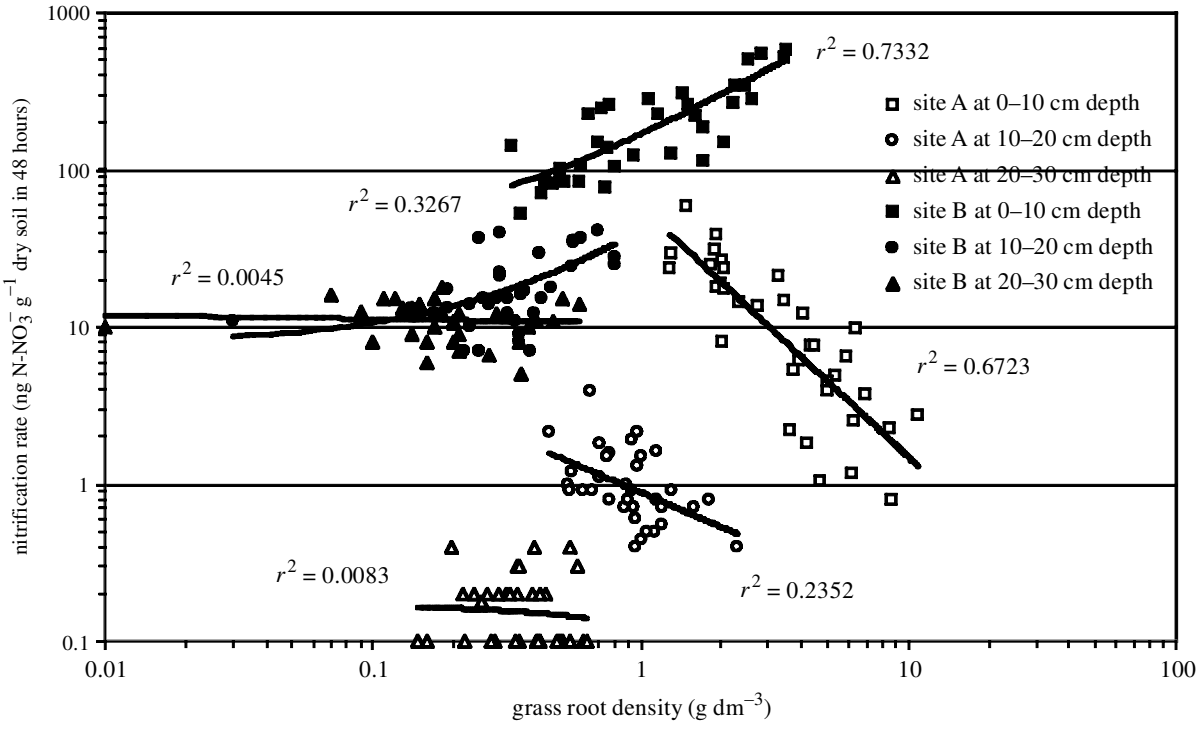

Figure 2. Relationships between grass root density and nitrification potentials at three depths (0–10, 10–20 and 20–30 cm) in the low nitrification and high nitrification sites. The grass root densities are expressed as g dm^{-3} dry soil. Nitrification is expressed as nanograms of NO_3^--N produced per gram of dry soil per 48 hours aerobic incubation. Note the logarithmic scale for the x- and y-axes; $n = 35$ for each treatment.

density and the nitrification potential in the 0–10 cm ($p = 0.0001$) and 10–20 cm ($p = 0.05$) soil layers. This correlation was negative in site A and positive in site B and clearly stronger in the 0–10 cm layer than in the 10–20 cm layer. No significant correlation could be established between the two variables in the deeper soil layer (20–30 cm).

4. DISCUSSION

(a) *Influence of* H. diplandra *tussocks on the nitrification potential on the site scale*

The values of the nitrate production observed in the site-scale sampling show that a considerable difference in nitrification status exists between the two sites. This confirms the results reported previously by Le Roux *et al.* (1995) and Lata *et al.* (1999) which described dual nitrogen cycling in the Lamto ecosystem. Moreover, the nitrification potential was significantly lower under than between the tussocks in the low nitrifying site while the opposite result was observed for the high nitrifying site. The results found for site A strengthen the hypothesis for direct control of nitrification by *H. diplandra*. This interaction could result from the production of allelopathic compound(s) by the roots of the site A subpopulation as previously suggested (Meiklejohn 1962, 1968; Munro 1966; Rice & Pancholy 1973; Lensi *et al.* 1992; Lata *et al.* 1999). The results found in site B need to be more deeply discussed. They strongly suggest that the roots of the *H. diplandra* subpopulation from site B are able to stimulate nitrification. This may appear surprising because, due to the autotrophic character of nitrification (Bock *et al.* 1989), this process is generally considered as not positively affected by root exudates. However, Lamto savannah presents peculiar organizational characteristics. Indeed, this ecosystem is highly structured and energy exchanges, micro-organisms and the production of organic and inorganic (such as ammonium, the substrate for nitrification) compounds are concentrated in the close vicinity of roots (Abbadie *et al.* 1992). Moreover, it is now known that nitrifiers are able to grow in mixotrophic or heterotrophic media (Bock *et al.* 1983) and to survive and multiply in soils under heterotrophic conditions (Degrange *et al.* 1997). The extremely contrasting chemical environments coexisting in the Lamto savannah (i.e. bare soil and under-grass soil exhibiting low and high nutrient concentrations, respectively) associated with the physiological properties of nitrifiers may explain why a higher nitrification potential could be clearly detected in the rhizosphere of the *H. diplandra* from the high nitrification site in this ecosystem.

(b) *Relationships between* H. diplandra *tussocks location, root density and nitrification potential on the decimetric scale*

The site-scale sampling described above demonstrated that the spatial variations in the low or high nitrification potentials at sites A and B, respectively, are partly driven by the *H. diplandra* distribution at each site, i.e. that the depleting or stimulating effects are strengthened in the root zone of *H. diplandra*. Based on this simple (binary) situation (presence or absence of roots), this suggests that the nitrification potential might be root-density dependent.

The nitrification potential of the superficial soil layer was horizontally variable on the decimetric scale at both

sites (transect sampling; figure 1). This variability was higher in the low nitrifying sites than in the high nitrifying sites (55- and sevenfold ratios were found between the maximal and minimal values in sites A and B, respectively), suggesting that the inhibiting impact on nitrification is more intense than the stimulating one. Similar values of spatial variability in nitrification have already been reported in temperate forest ecosystems, but they have been found at higher scales (Robertson 1982; Lensi *et al*. 1991). Moreover, we succeeded in identifying the density of roots as one of the main factors responsible for the small-scale spatial variability in nitrification. Indeed, clear negative or positive relationships (in sites A or B, respectively) exist between tussock location and root biomass on one hand and nitrification potential on the other. The high sensitivity of the nitrifying process to the density of roots in both inhibiting (site A) or stimulating (site B) configurations must be underlined: contiguous soil cubes may exhibit very different nitrification potentials along the transects in both sites (which is always satisfactorily related to a change in root density; figure 1). These data from the decimetric-scale samplings supply complementary arguments for supporting the hypothesis of direct involvement of *H. diplandra* in the regulation of the nitrifying process in the savannah ecosystem studied (Meiklejohn 1962, 1968; Munro 1966; Rice & Pancholy 1973; Lata *et al*. 1999). They also confirm that the decimetric scale is a relevant scale for studying the variability of the nitrifying process in such types of ecosystems and the cause of this variability.

The distribution of the nitrification potential was also found to be strongly affected by soil depth at both sites (figure 2). The decrease in the intensity of the process with depth has already been reported for other ecosystems such as temperate forests (Clays-Josserand *et al*. 1991). The influence of depth on nitrification and/or other microbial processes has been reported previously in the Lamto ecosystem (Pochon & Bacvarov 1973; Lensi *et al*. 1992; Nacro 1997). In the present study, the influence of soil depth on nitrification was very marked (0–10:20–30 cm soil layer ratio of 77 for the low nitrifying site and 19 for the high nitrifying site). The higher root density at site A compared to site B at all depths (figure 2) could be related to the higher basal cover of the grasses at site A compared to site B (J.-C. Lata, unpublished observations). A strong decrease in root density with soil depth was also observed at the two sites. This is consistent with previous results from the Lamto savannah, which reported the maximum grass root biomass in the first 10 cm (Menaut & César 1979).

The role of root density as one of the main factors involved in the regulation of the nitrifying process appears much more questionable in the deeper soil layers. Indeed, the correlation between the two variables became weaker in the 10–20 cm soil layer and practically disappeared in the 20–30 cm soil layer. Two non-exclusive hypotheses could explain this result: (i) factors other than plant roots became predominant in controlling nitrification in the deeper horizons, and (ii) the root-produced and/or -induced mediators involved in the inhibiting effect as well as in the stimulating one are too 'diluted' in the deeper layer to support any detectable interaction between the two variables.

In conclusion, the present study confirms that the Lamto savannah is a dual ecosystem according to its nitrification status and supports the hypothesis of a direct role of the grass *H. diplandra* in the control of nitrification. It also gives insight into the mode of plant–nitrification interaction by showing a close relationship between nitrification and root density for both inhibiting or stimulating influences. In fact, the impact of *H. diplandra* roots on nitrification may be viewed as an inhibition–stimulation balance under two hypotheses: (i) the *H. diplandra* plants at site A are only able to inhibit nitrification without any stimulating ability, and (ii) the *H. diplandra* plants at site A may exhibit both inhibiting and stimulating capacities, but the strong intensity of the inhibiting effect totally masks the stimulating one. Moreover, it cannot be excluded that different mechanisms of degradation of allelopathic compounds may exist in the two sites. Only the identification of the underlying mechanism(s) responsible for the inhibition may confirm or invalidate these hypotheses.

In order to prove the role of plants in the control of nitrification in the Lamto ecosystem definitively, the indirect approach based on the correlations used in the present study must be completed by direct approaches. Experiments based on (i) ecosystem manipulations, including transplantation of the two *H. diplandra* subpopulations into their own site and the other site, and (ii) *in vitro* evaluation of the influence of soil extracts from the two sites on pure cultures of nitrifiers are presently in progress.

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